

# The Spinifexbird *Eremiornis carteri* in the Desert Uplands Bioregion, north-central Queensland: a geographic isolate or a nomadic metapopulation?

A.S. Kutt

School of Tropical Biology and Australian Centre for Tropical Freshwater Research, James Cook University, Townsville, QLD 4811.

Current address: Queensland Parks and Wildlife Service (Environmental Protection Agency), PO Box 5391, Townsville MC, QLD 4810.

Email: Alex.Kutt@epa.qld.gov.au

## ABSTRACT

The Spinifexbird *Eremiornis carteri* is an inland species exclusively associated with mature *Triodia* spp. grasslands. Despite its wide distribution throughout arid and semi-arid Australia, a history of range expansion and contraction, and concentration into a number of core population centres, the species is considered monotypic. Two disjunct eastern localities were recorded during a vertebrate fauna survey of the Desert Uplands Bioregion in central-north Queensland, both in mature *Triodia longiceps* grasslands. These localities are described and reasons for the lack of speciation within this taxon are reviewed. Nomadism in response to fire and climate pressures, discrete habitat specificity and current land use patterns are discussed as possible causes of lack of morphological differentiation, though the possibility of cryptic genetic variation in sub-populations is canvassed.

**Key words:** Spinifexbird *Eremiornis carteri*, *Triodia*, metapopulation, nomadism, fire, genetic variation, Desert Uplands, Queensland

## Introduction

The Spinifexbird *Eremiornis carteri* is a small and secretive member of the passerine family Sylviidae or Old World Warblers. *Eremiornis* is a monotypic genus, though closely related to grassbirds *Megalurus* (Schodde and Mason 1999). As its common name implies, the Spinifexbird is strongly associated with the characteristic arid and semi-arid Australian hummock grasses ("spinifex") *Triodia* spp. More specifically its habitat is considered to be hilly, "uneven" country, above 300 m altitude, where run-off causes the *Triodia* and associated vegetation to grow thicker than elsewhere (Ford and Parker 1974). Distribution for this species generally follows a broad band between 20-25° latitude across central Australia from north-western Queensland to the Western Australian coast (Schodde and Mason 1999).

Within this zone, four major mainland populations are considered extant (central Western Australia, Fitzroy River drainage east to Victoria River, southern highlands of the Northern Territory and the Mt Isa-Opalton districts in Queensland), corresponding with sandstone ranges supporting the habitat described above (Ford and Parker 1974). Intervening areas of lower altitude sandy desert are considered to lack populations, or at least support very low numbers (Ford and Parker 1974), though historical records within these gaps have suggested a more continuous distribution, (Blakers *et al.* 1984; Schodde and Mason 1999).

Queensland populations were originally considered a subspecies *queenslandicus*, being smaller and less-rufous

(Mathews and Neuman 1939). Examination of Australia-wide material concluded that this interpretation was incorrect (Ford and Parker 1974), a decision recently reconfirmed (Schodde and Mason 1999). Spinifexbirds are generally considered sedentary (Ford and Parker 1974; Blakers *et al.* 1984; Pizzey and Knight 1997) and this somewhat confounds the conclusion that isolated populations are morphologically undifferentiated, in that many other central Australian bird species of comparable or smaller distribution have evolved distinct ultrataxa (Ford 1974; Schodde and Mason 1999).

In Queensland, the discovery of Spinifexbird distribution has been slow: a single collection from the Mt Isa-Cloncurry district that led to the proposal of a smaller Queensland subspecies (Mathews and Neuman 1939); further data for the Mt Isa district (Carruthers in Ford and Parker 1974); discovery of Spinifexbird populations at Opalton (Officer 1971); and additional reporting of localities in the Mt Isa (Horton 1975; Blakers *et al.* 1984) and Opalton-Winton regions (Dawson and Morgan 1974; Ford and Parker 1974; Blakers *et al.* 1984). In both areas populations are considered moderately common, sedentary and widespread (Horton 1975; Dawson and Morgan 1974) most typically in "thriving" *Triodia pungens* and *T. longiceps* grasslands (Ford and Parker 1974). This paper reports a further potentially disjunct population of the Spinifexbird in north-central Queensland, isolated from the nearest known localities at Opalton-Winton by a distance of over 200km (Fig. 1).

## Study area and methods

Distribution data for Spinifexbirds were collected from a fauna survey conducted within the Desert Uplands Bioregion (Fig. 1) between 1997 and 2000. This survey assessed variation of vertebrate species abundance and distribution in a range of regional ecosystem types (*sensu* Sattler and Williams 1999). The Desert Uplands is situated within Australia's northern tropical savannas, and straddles the Great Dividing Range between Charters Towers, Hughenden and Blackall, sharing boundaries with the Northern Brigalow Belt to the east and south, the Einasleigh Uplands to the north and the Mitchell Grass Downs to the west (Fig. 1). The climate is semi-arid, dominated by sandstone ranges and sand plains with soils of mostly poor structure and fertility comprising open *Acacia* and Eucalypt woodlands, ephemeral lake and dune systems and hummock and tussock grasslands (Sattler and Williams 1999).

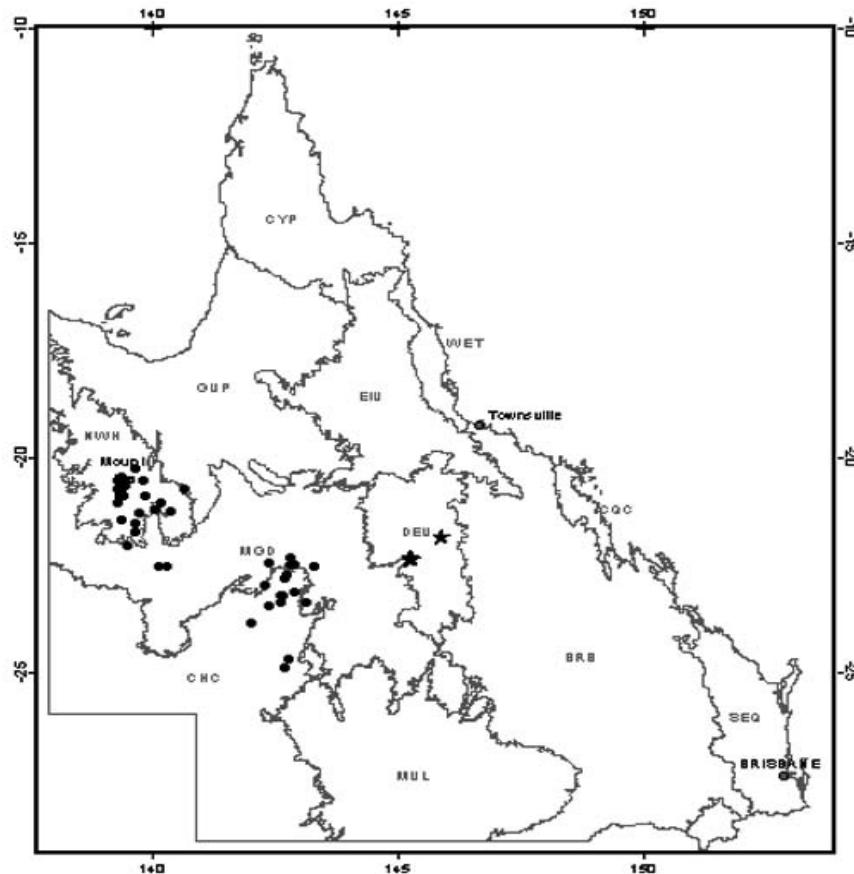
Sampling utilised a standardised nested quadrat array (1ha), modified from Woynarski and Fisher (1995), incorporating trapping (four pitfall and twenty small Elliott traps) and observation (bird counts and daily timed diurnal and nocturnal searches) over a 96 hours period. Bird counts consisted of four morning censuses undertaken on separate days within the survey period. Within the Desert Uplands, 158 quadrat sites were sampled, with 105 of these being sampled twice, each time in a different season.

## New Spinifexbird localities

Two discrete localities for Spinifexbird were located in the Desert Uplands Bioregion, approximately 100 km apart. Descriptions of these localities including vegetation and general habitat features are as follows.

### Moonoomoo Station ( $21^{\circ} 52' 4.8''$ $146^{\circ} 1' 55.2''$ ) 120 km south-east of Charters Towers

Open hummock grassland *Triodia longiceps* to 0.75 m and 50% cover, with scattered Yapunyah *Eucalyptus thozetiana* to 14 m. Virtually a monoculture of *Triodia* in the ground cover, though the grass *Sporobolos actinocladus* appears in small patches. Remainder of ground cover approximately 25% bare and 25% small rocks (ironstone) to 6 cm. Soils red sandy-clays and poorly drained. Altitude 300-350 m. The *Triodia* patch was no more than 10 ha in size but embedded within a mosaic of other hummock grassland patches, open woodlands of *E. thozetiana*, Mallee box *E. persistens* and Reid River Box *E. brownii* all with mixed *Triodia* spp. and tussock grass ground cover and low woodlands of Blackwood *Acacia argyrodendron*, Lancewood *A. shirleyi* and Gidgee *A. cambagei*. This site is moderately grazed and rarely burnt except by wildfire, though exact information is not available. It is directly adjacent to, and fenced from, extremely fertile and heavily grazed *E. brownii*, *E. thozetiana* and *A. cambagei* on clay soils. The



**Figure 1.** Distribution of the Spinifexbird in Queensland identified by existing published point records. Solid circle indicates records prior to this study. Sources are literature in text, Queensland Museum, and data from the Birds Australia Atlas of Australian Birds (Blakers et al. 1984). Solid star represent new records for the Desert Uplands Bioregion. Bioregion abbreviations: MGD = Mitchell Grass Downs, DEU = Desert Uplands, BRB = Brigalow Belt, CHC = Channel Country, MUL = Mulga Lands, NWH = North-west Highlands.

quadrat site was visited three times and sampled for two days in August 1998 (during a reconnaissance trip), four in November 1998 and four September 1999. Spinifexbirds were recorded only in the latter two surveys and were most vocal and prominent in November, coincident with known breeding period (August to November, Pizzey and Knight 1997). At least two, and possibly four individuals were noted.

### **Albionvale Station (22° 20' 42.1" 145° 24' 24.2") 100 km north of Aramac**

Open hummock grassland *Triodia longiceps* to 0.5 m and 40% cover. Additional ground cover to 10% composed of tussock grasses *Eragrostis speciosa*, *Dactyloctenium radulans*, *Sporobolus actinocladus*, forbs *Polycarpaea corymbosa*, *Trianthema triquetra*, *Salsola kali*, and sedges *Fimbristylis bisumbellata*. Remaining 50% bare. Soils shallow white sandy-clays overlying deep grey clays, also poorly drained. Altitude 250 m. This area supports large *Triodia* grasslands within a mosaic of herb-fields, heaths and artesian mound springs which form an extensive (>8000 ha) low altitude, saline discharge zone on the western edge of the Desert Uplands and a significant inflow area for the Great Artesian Basin (Morgan *et al.* 2000). This site is heavily grazed and regularly burnt, though exact stocking rates and fire frequency are again unknown. Adjacent areas of low open woodlands on sandy clays have been extensively cleared on this property. The site was visited twice and sampled for four days in July 1999 and four days in February 2000. Spinifexbirds were recorded only February, though were very elusive and rarely vocal. At least two individuals were recorded for the site.

### **Discussion**

The location of these Spinifexbirds as a geographic isolate follows the established pattern for the species, appearing in disjunct sandstone habitats with extensive *Triodia* grasslands and associated woodland vegetation. The Desert Uplands is separated from the nearest populations in the Opalton-Winton area by a large expanse of low altitude *Astrebla* spp. and associated grasslands on cracking clays in the Mitchell Grass Downs Bioregion. Though perhaps unexpectedly further east, the presence of appropriate vegetation types and new localities geographic position on the eastern edge of the broad Eyrean zone suggests the Spinifexbird's appearance and continuous distribution is predictable.

The Moonoomoo Station location lies directly on the Great Dividing Range, clearly on the border of the Eyrean and Torresian zones. This locality must surely represent the Spinifexbirds' most eastern locality, as beyond this point climate, altitude and vegetation shifts markedly into wetter savanna woodlands. The locations at Albionvale Station were less surprising, this region having more extensive *Triodia* vegetation that is typical of the Channel Country near Winton-Opalton, and a direct geographic and hydrological relationship with the Great Artesian Basin. Other species recorded here are also more typically arid-zone, including Centralian Blue-tongue Lizards *Tiliqua multifasciata*, White-winged Fairy-

wrens *Malurus leucopterus* and Desert Mouse *Pseudomys desertor*. The last species in some ways parallels the Spinifexbird discovery in the Desert Uplands. Previously considered rare and poorly known in Queensland, and presumed to be restricted to arid western Queensland in the Channel Country and North-west Highland Bioregions, *P. desertor* was the most common and abundant terrestrial rodent trapped in this study, and was strongly affiliated with *Triodia* spp. vegetation communities (unpubl. data).

Though only recorded in two discrete localities, potential habitat for the species in the Desert Uplands is moderately extensive. There are small and patchy, but widespread, *Triodia longiceps* grasslands predominantly distributed in the western portion of the bioregion, and extensive *T. pungens* dominated grasslands and woodlands throughout the central Alice Tablelands. However, in the latter community, the combination of grazing and fire may create a low, quite sparse ground cover, perhaps unsuitable for Spinifexbirds. Over 50 quadrats were sampled in *Triodia* spp. communities and Spinifexbirds were recorded only in the *T. longiceps* grasslands. The more resilient dense structure of *T. longiceps* and its relative unpalatability to stock compared to *T. pungens* which is grazed and regularly burnt, may provide a more consistent habitat refuge.

Eyrean avifauna is thought to have Bassian, Torresian and *in situ* origins (Schodde 1982), the primary derivation of most species being from the mesic south-west Bassian and the tropical north-east Torresian environments (Schodde 1982). Isolation, via geographic barriers, migrating founders, stranding within refugia, and followed by subsequent habitat adaptation, is considered the primary cause for arid/semi-arid avian speciation (Ford 1974; Schodde 1982; Ford 1987). Continued patchiness of extant Eyrean species is thought to be directly due to this historical adaptation to specific substrates and resources, a pattern reinforced by intervening areas of inappropriate habitat (Schodde 1982; Ford 1987).

The Spinifexbird is one of the few monotypic Eyrean bird species, despite a clear habitat specificity and a history of range expansion and contraction (Ford and Parker 1974). Its existence in a series of primary refuges (Selwyn Ranges/Mt Isa-Opalton Plateau, Hammersley and Pilbara Ranges, Central Australian ranges) (Schodde 1982; Ford 1987; Schodde and Mason 1999) on face value suggests that the undifferentiated status for the Spinifexbird is ecologically somewhat paradoxical, though clear morphological evidence exists for its singular status (Ford and Parker 1974; Schodde and Mason 1999). Four broad explanations for this pattern have been, or are proposed: Spinifexbirds in Australia consist of a nomadic metapopulation; being of Eyrean origin they have failed to differentiate during periods of Pleistocene aridity; there are possibly unidentified cryptic species within the population that exhibit no morphological variation; and that post-European land management impacts have increased population discontinuity. Each is discussed in further detail below.

## Nomadic metapopulation

Pan-arid zone nomadism and post-rainfall irruption from core habitats and consequent genetic interchange are identified as a possible cause for lack of speciation in the Spinifexbird (Ford 1974), an explanation provided for the monotypic status of the Crimson Chat *Epthianura tricolor* (Keast 1958). This is a typical metapopulation pattern, where genetically identical sub-groups interact, but are geographically separated (Hanski and Gilpin 1991). The wide geographic separation for such a terrestrial and cryptic bird seems problematic, though Old World Warblers from which Spinifexbirds derived, are renowned for their migratory prowess (Schodde and Mason 1999). The suggestion is that, despite its small size and apparently weak power of flight, a capacity for longer-distance dispersal may remain. Historically irregular rainfall and large scale habitat patchiness caused by traditional burning of landscape by Aboriginal people may have reinforced this nomadic behaviour.

There is little available information regarding the relative flight abilities of Spinifexbirds in comparison to other warblers and grassbirds, sedentary species of the arid interior (e.g. *Malurus*, *Amytornis*) and other arid nomads (e.g. Crimson Chat, *Epthianura tricolor*), though the related Little Grassbird *Megalurus gramineus* has successfully colonised artesian bores in the arid inland (Blakers *et al.* 1984) implying dispersal ability. Limited data in Ford and Parker (1974) and Higgins *et al.* (2001) indicate absolute wing lengths of Spinifexbirds (51-53.5 mm) to be longer than those of fairy-wrens (e.g. *Malurus leucopterus* 43-47.3 mm) and emu-wrens (e.g. *Stipiturus ruficeps* 36-39.5 mm), equable to those of grasswrens (e.g. *Amytornis striatus* 53.5-56 mm) and shorter than those of chats (e.g. *E. tricolor* 64.3-67.5 mm), suggesting an intermediate flight ability. Data on relative wing length, which also reflects bird shape and size, is a better predictor of distance flight (W. Boles, Australian Museum, pers. comm., 2002). Examination of the length sequence of the five outer wing primaries (highest is the outermost) indicates the following pattern: Superb Fairy-wren *Malurus cyaneus* ( $7=6=5=4>3$ ); Striated Grasswren *Amytornis striatus* ( $7=6=5\geq 4>3$ ); Little Grassbird *M. gramineus* ( $8=7=6=5>4$ ); *Eremiornis carteri* ( $8=7=6=5>9$ ); and Crimson Chat *Epthianura tricolor* ( $8>7>9>6>5$ ) (Higgins *et al.* 2001; W. Boles, Australian Museum, pers. comm., 2002). Therefore morphologically, fairy-wrens and grasswrens have short, rounded wings (longest primaries 5-7), while nomadic Crimson Chats have long pointed wings (longest primaries 7-9). Spinifexbirds have wings similar in shape to that of the Little Grassbird, intermediate to grasswrens and chats, suggesting some dispersal ability.

For comparison, wing-aspect loading and flight characteristics of microchiropteran bats have been well studied (e.g. Bullen and McKenzie 2001 and references therein) indicating slow flying, manoeuvrable gleaners (e.g. *Nyctophilus*) have short broad wings whereas fast flying, above canopy species (e.g. *Tadarida australis*, *Taphozous* spp.) have long narrow wings. The latter species are known and expected to seasonally migrate or travel long nightly distance to feed

(Churchill 1998), however *Nyctophilus geoffroyi* has also been recorded flying an unexpected 10 km per evening, between roosts and remnant foraging habitat (Lumsden *et al.* 1995). This suggests that though wing structure controls typical flight and foraging patterns of volant species, it may not be a limiting factor on the ability to disperse or migrate within a heterogeneous terrestrial landscape, given the appropriate reason. Higgins *et al.* (2001) identifies some secondary sources that suggest species such as White-winged Fairy-wren *Malurus leucopterus* can be locally nomadic, moving seasonally.

## Eyrean origin and the failure to differentiate

The Spinifexbird is considered of Eyrean origin, derived from ancestral warbler populations entering Australia from the north-west (Schodde 1982). This obviously implies primary or *in situ* adaptation to arid landscapes. Subsequent expansion with increasing aridity in Australia, followed by contraction and isolation has left sub-populations in areas of habitat to which Spinifexbirds have already well adapted, but without impetus for morphological change, as happened to mesic Bassian or Torresian species isolated into xeric environments (e.g. *Gerygone fusca* and *G. olivacea*, Ford 1974). Potential expansion of Spinifexbirds into eastern wet-dry grasslands was not possible due to the existing radiation into these niches by other Old World Warbler descendants of *Acrocephalus* and *Megalurus* (Schodde and Mason 1999) from an existing Torresian origin.

## Cryptic species with no morphological variation

Morphological variation in the Spinifexbird has been examined twice, both concluding its monotypic status (Ford and Parker 1974; Schodde and Mason 1999). Molecular evidence also exists as to its interspecific relationships, confirming the unique generic status of *Eremiornis*, and its phylogenetic position next to *Megalurus* (Schodde and Mason 1999). This situation is not unique as both the Yellow White-eye *Zosterops luteus luteus* and Crimson Finch *Neochmia phaeton* in northern Australia have widely disjunct populations with no morphological variation (Schodde and Mason 1999). However there apparently has been no intraspecific genetic examination of the Spinifexbird and it is possible there are cryptic ultrataxa within population isolates, which lack morphological distinction. Molecular studies using mitochondrial DNA have identified deep genetic differentiation in species that lack any external phenotypic variation across vicariant rainforest refugia (Chowchilla *Orthonyx spaldingii*, Grey-headed Robin *Poecilodryas albispecularis* Joseph *et al.* 1995; Moritz *et al.* 1997), though Schodde and Mason (1999) subsequently identified a northern form of Chowchilla on morphological grounds. Conversely, rainforest generalists which exhibit greater flexibility in habitat preference lacked genetic differences between isolated populations (e.g. White-browed Scrubwren *Sericornis frontalis laevigaster*, Joseph *et al.* 1993; Schodde and Mason 1999). Recently other species of inland birds geographically isolated but with no obvious morphological variation have been found to have genetically differentiated populations (L. Christidis, Museum Victoria, pers. comm.).

## Post-European impacts

The impact on native fauna by post-European landuse - grazing by hoofed stock, alteration of traditional fire regimes and the ancillary increase in feral predator numbers - is well accepted (Burbidge and McKenzie 1983; Morton 1990). Grazing impacts were recognised as responsible for the demise of terrestrial mammal species as early as the 19<sup>th</sup> century (Krefft 1866). It is possible that the extant pattern of Spinifexbird isolates in rough, hilly terrain is partly a function of this more recent history. Intermediate *Triodia* and tussock grass habitat may have been transitory or non-core habitat, but still utilised sporadically or for regular migratory movement. Decrease in the density and cover of the ground strata by grazing, and discontinuation of traditional burning by Aboriginal people, decreasing the frequency and patchiness of the fire mosaic and increasing scale and intensity of the impact (Burbidge and McKenzie 1983) may have accentuated both the isolation and the gaps, and therefore a pattern of patchy distribution.

## Conclusion

North-eastern Queensland, including the northern Desert Uplands, is an area of remarkable avian hybridisation and ultrataxa radiation (Keast 1961; Schodde and Mason 1980, 1999; Schodde 1982; Ford 1986, 1997). The identification of a population of Spinifexbird in the Desert Uplands extends the eastern range extent for this species, but the disjunction suggests the habitat in this bioregion may currently or historically have acted as a refuge. The intergradation of a number of Eyrean and Torresian fauna species and the presence of two new, seemingly endemic species of reptile (Couper *et al.* 2002; unpubl data) further supports the biogeographic significance of this area.

A definitive assessment of the nature of the Spinifexbird population in the Desert Uplands is not possible from simple observations of two new localities. Large areas of suitable habitat exist and remain unsurveyed, and these records suggest this bioregion may support another Spinifexbird isolate, but part of a larger metapopulation connected by recent or past nomadic migration either from the Opalton-Winton district to the west or the Mt Isa region to the north-west. Though it is presumed the Spinifexbirds in the Desert Uplands have been extant for a long period, the coincidence of these records with a period of record rainfall in central and western Queensland cannot discount the possibility of very recent migration to the Desert Uplands. No historical data exist to confirm this, and both the Desert Uplands and adjacent Einasleigh Uplands Bioregions remain poorly surveyed and warrant further attention.

On evidence presented above, it is suggested that, though Spinifexbird populations are clustered into areas of ideal habitat, changing local conditions over the short or long term are likely to promote a degree of nomadism. Past and current patterns of rainfall variability, the pattern of large fires in *Triodia* communities, and an association with lush, mature *Triodia* indicate a species that needs to be flexible and mobile. The map of Spinifexbird localities in Queensland (Fig. 1) indicate that the population at Mt Isa and Winton are also divided by the Mitchell Grass Downs (with a couple of isolated intermediate records), a pattern similar to the southern cluster and the Desert Uplands records. This suggests barriers of such distance, though perhaps accentuated by current land use, are negligible. Following this, it is predicted that within Queensland there is likely no genetic variation in the species. However, across its entire distribution in Australia where the scale of geographic distances may be more influential, there is still a likelihood of cryptic genetic difference between Western and Central Australian and Queensland populations.

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## References

- Blakers, M., Davies, S.J.J.E and Reilly, P.N. 1984. *The Atlas of Australian Birds*. Melbourne University Press, Melbourne.
- Bullen, R. and McKenzie, N.L. 2001. Bat airframe design: flight performance, stability and control in relation to flight. *Australian Journal of Zoology* 49: 235-261.
- Burbidge, N. T. and McKenzie, N. L. 1983. Patterns in the modern decline of western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* 50: 143-198.
- Churchill, S. 1998. *Australian Bats*. Reed New Holland, Sydney.
- Couper, P.J., Amey, A.P. and Kutt, A.S. 2002. A new species of the genus *Ctenotus* (Scincidae) from Central Queensland. *Memoirs of the Queensland Museum* 48: 85-91.
- Dawson, P.E. and Morgan, B. 1974. An ornithological tour of western Queensland. *Sunbird* 5: 57-64.
- Ford, J. 1974. Speciation in Australian birds adapted to arid habitats. *Emu* 74: 161-168.
- Ford, J. 1986. Avian hybridisation and allopatry in the region of the Einasleigh Uplands and Burdekin-Lynd divide, north-eastern Queensland. *Emu* 86: 87-110.

- Ford, J.** 1987. Minor isolates and minor geographical barriers in avian speciation in continental Australia. *Emu* 87: 90-102.
- Ford, J. and Parker, S.A.** 1974. Distribution and taxonomy of some birds from south-western Queensland. *Emu* 74: 177-194.
- Hanski, I. and Gilpin, M.** 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42: 3-16.
- Higgins, P.J., Peter, J.M. and Steele, W.K. (eds.)** 2001. *Handbook of Australian and New Zealand Birds. Volume 5 Tyrant-flycatchers to Chats*. Oxford University Press, Melbourne.
- Horton, W.** 1975. The birds of Mt Isa. *Sunbird* 63: 49-69.
- Joseph, L., Moritz, C. and Hugall, A.** 1993. A mitochondrial DNA perspective on historical biogeography of mideastern Queensland rainforest birds. *Memoirs of the Queensland Museum* 34: 201-214.
- Joseph, L., Moritz, C. and Hugall, A.** 1995. Molecular support for vicariance as a source of diversity in rainforest. *Proceedings of the Royal Society of London B.* 260: 177-182.
- Keast, A.** 1958. The relationship between seasonal movements and the development of geographic variation in the Australian Chats *Epthianura* Gould and *Ashbyia* North Passeres: Muscicapidae, Malurinae. *Australian Journal of Zoology* 6: 51-68.
- Keast, A.** 1961. Bird speciation on the Australian continent. *Bulletin of the Museum of Comparative Zoology* 123: 307-495.
- Krefft, G.** 1866. On the vertebrate animals of the lower Murray and darling, their habits, economy, and geographical distribution. *Transactions of the Philosophical Society of New South Wales*. 1862-1865: 1-33.
- Lumsden, L.F., Bennett, A.E., Krasna, S.P. and Silins, J.E.** 1995. The conservation of insectivorous bats in rural landscapes of northern Victoria. Pp. 142-148 in *People and Nature Conservation: Perspectives on Private Land Use and Endangered Species Recovery*, edited by A. Bennett, G. Backhouse and T. Clark. Royal Zoological Society of New South Wales, Mosman, NSW.
- Mathews, G.M. and Neumann, O.** 1939. Six new races of Australian birds from north Queensland. *Bulletin of the British Ornithological Club* 59: 153-155.
- Morgan, G., Lorimer, M., Morrison, A. and Dahl, T.** 2000. *The Desert Uplands Draft Bioregional Conservation Strategy*. Environment Protection Agency, Townsville.
- Moritz, C., Joseph, L., Cunningham, M. and Schneider, C.** 1997. Molecular perspectives on historical fragmentation of Australian tropical and subtropical rainforests: implications for conservation. Pp. 442-454 in *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*, edited by W.F. Laurence and R.O. Bierregaard Jr. University of Chicago Press, Chicago.
- Morton, S.R.** 1990. The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. Pp. 201-213 in *Australian Ecosystems: 200 years of Utilisation, Degradation and Reconstruction. Proceedings of the Ecological Society of Australia*, vol. 16, edited by D.A. Saunders, A.J.M. Hopkins and R.A. How. Surrey, Beatty and Son, Chipping Norton, Sydney.
- Officer, H.R.** 1970. The Spinifexbird at Opalton. *Sunbird* 2: 79-80.
- Pizzey, G. and Knight, F.** 1997. *The Field Guide to Birds of Australia*. Harper Collins Publishers, Sydney.
- Sattler, P. and Williams, R.** 1999. *The Conservation Status of Queensland's Bioregional Ecosystems*. Environmental Protection Agency, Brisbane.
- Schodde, R.** 1982. Origin, adaptation and evolution of birds in arid Australia. Pp. 191-224 in *Evolution of the Flora and Fauna of Arid Australia*, edited by W.R. Barker and P.J.M. Greenslade. Peacock Publications, South Australia.
- Schodde, R. and Mason, I.** 1980. *The Nocturnal Birds of Australia*. Landsdowne Press, Melbourne.
- Schodde, R. and Mason, I.** 1999. *The Directory of Australian Birds: Passerines*. CSIRO, Collingwood.
- Woinarski, J.C.Z. and Fisher, A.** 1995. Wildlife of lancewood (*Acacia shirleyi*) thickets and woodlands in Northern Australia. 1. Variation in vertebrate species composition across the environmental range occupied by lancewood vegetation in Northern Territory. *Wildlife Research* 22: 379-412.